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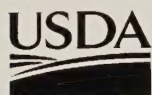
Proceedings of the Southern Appalachian Biological Control Initiative Workshop



Phillip Gibson
Charles R. Parker

Forest Health Technology Enterprise Team

Morgantown, WV



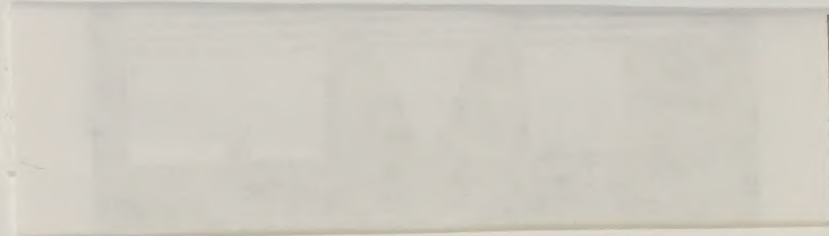
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Cover photo: White ovisacs are very apparent and an easy way to identify trees infested with hemlock woolly adelgid.



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Proceedings of the Southern Appalachian Biological Control Initiative Workshop

Asheville, North Carolina

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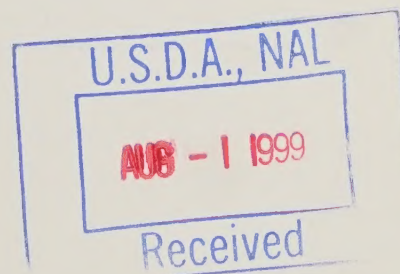
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- The Great Smoky Mountain National Park staff—Keith Langdon and Joe Abrell (who together initiated the Southern Appalachian Biological Control Initiative workshop), Kristine Johnson, Glen Gaines, and Superintendent Karen Wade—for their guidance, assistance and insight; and
- The NC Arboretum staff—George Briggs, Executive Director, and Laura Johnson—for providing us with an appropriate and outrageously beautiful site for the workshop.
- Special thanks to the participants and speakers who presented their research and ideas. Through participatory discussions and information sharing, they assisted in furthering the cooperative spirit needed for addressing the complexities of all ecosystems. The speakers were Ernest Delfosse, Scott Schlarbaum, Roy Van Driesche, Gary Johnston, Faith Campbell, Randy Westbrook, Bill MacDonald, Mark Windham, Dave Houston, Bob Anderson, Mike Montgomery, Richard Reardon, and Roger Fuester.

Phill Gibson
Environmental Planner
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Contents

Summary of Workshop and Conclusions	1
Biological Control of Arthropod Pests of the Northeastern and Northcentral Forests in the United States: A Review of the Literature and Identification of Future Opportunities	
R.G. Van Driesche, S. Healy, R. Reardon	7
Exotic Plants and Biocontrol	
Faith Thompson Campbell	15
Biological Approaches to Chestnut Blight Control	
William L. MacDonald	19
Potential for Biologically Based Control of Beech Bark Disease in the Southern Appalachians	
David R. Houston	23
Butternut Canker	
Robert L. Anderson, Scott E. Schlarbaum, Pauline C. Spaine	33
Biological Control of the Gypsy Moth: An Overview	
Richard C. Reardon	39
Woolly Adelgids in the Southern Appalachians: Why they Are Harmful and Prospects for Control	
Michael E. Montgomery	47
List of Acronyms	59

Chuck Parker of the former and Phillip Gibson of the latter, this workshop disseminated and shared information on the history of major invasions of exotic insects, diseases, and plants which affect the southern Appalachians and on management strategies for the biological control of these exotics.

Funding

Issues raised by the impacts of exotic species reach beyond political, disciplinary, economic, or agency boundaries. Therefore, the organizers of this workshop sought collaboration by a number of experts from a variety of disciplines in both the public and private sectors. Funding for this collaborative workshop came jointly from the USGS BRD and a grant to SAMAB from the USDA National Biological Control Institute (NBCI).

USGS BRD's directive for "The Southern Appalachian Biological Control Initiative" is the outgrowth of a BRD grant, "Initiate Biological Control of Forest Pests." The proposal for this grant originated in the Great Smoky Mountains National Park of the National Park Service. The BRD Natural Resources Protection Program funded the proposal, making a grant to the Southern Appalachian Field Laboratory (SAFL) of the Leetown Science Center. Chuck Parker, of the Great Smokies Field Station, an office of the SAFL, developed the work plan. The proposal calls upon BRD to establish a mechanism to coordinate the needs of Department of Interior (DOI) land managers for biological control. The authors of the proposal suggested that biological control practitioners, who traditionally are supported to study agriculturally or economically important species, were giving biological control of many serious exotic forest pests less emphasis than is warranted.

To ensure that the goals of the original proposal were met, the work plan called for a series of regional workshops to identify and rank the most serious exotic pests in each region. The authors of the work plan concluded that a regional approach was necessary to prevent species that have invaded tens of thousands of hectares in one region, such as tamarisk in the West or melaleuca in South Florida, from overshadowing the pests of other regions in importance. The regional approach required input from land managers of national parks and forests, as well as from managers of state, private, and commercial lands. After ranking the pests according to the threat they present to the resource, the plan prioritized them according to their potential as targets of biological control. This process required the participation of authorities in biological control who could address those questions. Finally, the workshop participants were asked to recommend a plan of action to implement biological control against the targeted pest(s).

The initial workshop was held at the North Carolina Arboretum in Asheville, North Carolina. The SAMAB Program obtained additional financial support for the workshop from the NBCI, a entity of the U.S.

Department of Agriculture's Animal and Plant Health Inspection Service (APHIS).

Workshop Findings

Thirty-two federal, four state, six private, and 11 university representatives participated in the two-day workshop (see the attached attendance sheet). The first day was devoted to discussions of the most recent developments in biological control, invasive species, and DOI policies. On the second day, participants were assigned to one of six work groups which were organized to ensure that each group had a good mix both of land managers and technical authorities, and of federal, state, private, and university participants.

The work groups were charged with identifying the most serious exotic pests in the region and ranking them according to their threat to the resource. Group leaders recorded the choices and the justifications for each choice. When the groups reconvened and compiled the rankings, it was found that each group had chosen hemlock woolly adelgid as the most significant threat facing Southern Appalachian forests. The choices for second and third most serious pests were also broadly, though not unanimously, supported. These were, respectively, balsam woolly adelgid and beech bark disease. Butternut canker was ranked fourth.

Another interesting result of the ranking exercise was that kudzu, an exotic vine that grows over all obstacles in its path throughout the Southeast, was chosen by two groups as the number one "public interest" pest. These groups felt that kudzu is perhaps the most visible and widely recognized pest in the region. Any effort to control kudzu, therefore, would generate tremendous public interest, serve as a valuable public education tool, and help generate additional funding.

Similar sentiments were expressed about the restoration of American chestnut. This tree was once one of the most important hardwood species in the region, before chestnut blight all but eliminated it from the forests. It now exists only as sprouts from still viable root stocks, but even these sprouts succumb to the blight before they can reach maturity. As with kudzu, the work group felt that any efforts on behalf of American chestnut would generate valuable public support for biological control and would help generate additional funds for further research. Thus, kudzu was ranked the fifth, and chestnut blight the sixth, most serious pests.

After identifying and ranking the most serious pests in the region, it was necessary for workshop participants to examine the pests and determine the potential for each as a target of biocontrol efforts. Following this determination, participants prioritized the pests according to their severity ranking and their potential for control. The distinction between ranking and priority is important. The potential of a species as a target of biological control is not necessarily a reflection of its status as a pest. A pest that poses a relatively minor threat to an ecosystem may nevertheless

have excellent prospects for successful biological control. Alternatively, there may be little or no prospect for successful biological control of a serious threat to ecosystem integrity. Therefore, prioritizing pests once they have been ranked may result in a different ordering of the species. This difficult process was debated for some time. Arguments were presented for and against each pest, and the pros and cons were tabulated. Finally, the group arrived at the consensus that hemlock woolly adelgid was the highest priority pest in terms of its potential for successful biological control as well as the highest ranked pest in terms of its threat to the resource. However, the potential for and the value of chestnut restoration, and the prospects of accomplishing something meaningful against kudzu, resulted in those species being prioritized second and third, respectively, despite their lower ranking in terms of seriousness.

In addition to their consensus on the top priority of hemlock woolly adelgid, the workshop participants agreed nearly unanimously that public education on these issues is a paramount need. It is the opinion of the participants that without strong educational efforts to support controls that might prevent additional threats from becoming established in this country, the battle against exotic species may not be winnable. In addition, it is the opinion of the participants that biological control is perhaps the single best option for long-term control of widespread pest species. Public support for this approach is vital if it is to succeed, and education is essential to achieve that support.

Plan of Action

The final task of the workshop was to recommend a plan of action. The BRD grant provided \$75,000 in fiscal year 1997 and \$125,000 in fiscal year 1998. The participants examined the priority list of species and the need for education and recommended the following:

- A total of \$140,000 should be earmarked for research on hemlock woolly adelgid.
- Kudzu and chestnut blight research should be supported at \$20,000 each, at \$10,000 each per fiscal year.
- \$20,000 should be set aside for education, pending the approval of matching funds from other agencies and organizations. In the unlikely event those funds are not forthcoming, the money should go to the adelgid research.

The participants expressed satisfaction at the outcome. The organizers felt the process worked very well, and that the mix of people from different agencies and backgrounds was an important part of the success. Among federal agencies, representatives of the National Park Service, the Fish and Wildlife Service, the USDA Forest Service, the NBCI, and the USDA Agricultural Research Service indicated enthusi-

asm for the program and a desire to continue to participate with BRD on biological control and exotic species issues. Representatives of state forestry and biocontrol agencies also were strongly supportive, as were representatives of SAMAB and The Nature Conservancy.

An important goal of the original proposal was to establish a mechanism within DOI to coordinate the department's needs for biological control. We believe that the concept of holding regional workshops and building networks of land managers and biocontrol practitioners within ecoregions is a good basis for developing such a mechanism. Funding opportunities for research on biological control of exotic species are limited. By combining resources from different agencies and leveraging funding from a variety of sources, DOI can help ensure that the concerns of its land managers are addressed by the biological control community.

Conclusion

Both the spread and impacts of exotic species are expected to increase. Non-native species continue to be promoted by the private sector (i.e., the nursery industry) as well as some government agencies. However, future funding for research on biological control (i.e., post-release monitoring) continues to be limited.

These and other reasons support the conclusion that there is a dire need to build regional mechanisms throughout the United States which will promote collaboration, both technical and fiscal, to address exotic species and their management strategies. Success will also depend upon including the private sector in all ventures. As is the case with southern Appalachia, less than 18% of the land is owned or managed by the public sector. Additionally, southern Appalachia is impacted by land, forest, and ecosystem management applied to the larger region of the eastern United States. Therefore, a comprehensive education program is needed to address both the potential hazards of exotic species and appropriate strategies to ameliorate their current and future impacts.

As a result of the workshop, Phillip Gibson formed an education strategy committee to address the need for public education. This committee is composed of technical and educational professionals from both the public and private sectors. Given the history of some species introductions, the committee views as its primary objective education about and promotion of native plant use with both the nursery industry and consumers. The goals of this effort are obviously both complex and long-term. The committee is seeking multi-year funding to fulfill its objectives.

Comments

Any goal of this or future initiatives must include representatives of all sectors and interested parties. The complexity and scope of work will be tremendous; success will require the technical and fiscal support of everyone. Experts from all disciplines of the biological and social sciences

should be included. For example, managers of human health have not traditionally been involved in ecosystem management. But land management can play a significant role in the emergence and reemergence of infectious diseases. In fact, the Office of Technology Assessment has documented the human health risks of some kinds of biological control.

Political, scientific, fiscal, and other boundaries are potential obstacles we must work to overcome. Accomplishing the goals of biological control in this manner will promote true ecosystem management.

Biological Control of Arthropod Pests of the Northeastern and Northcentral Forests in the United States: A Review of the Literature and Identification of Future Opportunities

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The objective of this review of literature on 94 species of arthropod forest pests was to summarize current knowledge about the role of biological control in the population dynamics of these pests for the purpose of identifying which species are the best candidates for future, new, or reopened biological control projects. This report identifies species for which opportunities exist for the use of biological control by means of natural enemy importation, conservation, or augmentation. Other species reviewed were felt to be not as suitable as biological control targets. This information is summarized in Tables 1 through 4.

Summary of Recommendations

This report reviews 94 species of forest arthropods. Other species than those reviewed here may be important pests from the perspective of more particular geographic areas or tree species. Consideration of the potential for application of biological control in such cases will require further review.

Fifty-eight of the species reviewed (62%) are believed to be native to North America. The origins of two species, spruce mite and larch sawfly, (2% of the species reviewed) are uncertain or disputed. The

remainder of the reviewed species include 29 species (31% of the total reviewed) of non-native origin currently found in North America and three species (3%) not yet present in North America, but of concern. The latter are *Ips typographus*, *Sirex noctilio*, and *Lymantria monacha*. Finally, three species (Cooley spruce gall adelgid, Nantucket pine tip moth, and tuliptree aphid) are native North American species that have spread into regions of North America outside their original ranges, and thus occur as non-native species in some areas.

The concluding paragraphs of each species' section of this report give detailed recommendations of how biological control might be employed for the control of these pests. These recommendations are grouped into the following categories, corresponding to the likelihood of success and methods of employing biological control.

- Natural enemy introductions
- Augmentation of natural enemies through artificial propagation and release
- Studies of population dynamics to clarify importance of natural enemies or identify modifications of silvicultural practices that enhance effects of existing natural enemies at production sites
- No role for biological control.

Natural enemy introductions

Of the 29 species of non-native pests reviewed, 27 were judged to provide opportunities for their control via natural enemy introductions (see Table 1, opposite).

Table 1. Species for which introductions of new species of natural enemies are needed or for which introductions of natural enemies which previously controlled the pest are needed			
Species	Pest Number	Pest Origin	Natural Enemy Needed, or Area to be Explored
1. eastern spruce gall adelgid	3	E	<i>Aphidoletes abietus</i>
2. balsam woolly adelgid	4	E	explore Caucasus Mountains
3. hemlock woolly adelgid	5	E	explore China and Japan
4. Cooley spruce gall adelgid	6	N (but E in eastern N.A.)	explore Colorado
5. woolly beech aphid	11	E	determine native range
6. tuliptree aphid	12	N (but E in CA)	explore eastern U.S.
7. Norway maple aphid	13	E	explore Europe
8. linden aphid	14	E	explore China
9. beech scale	15	E	determine native range
10. red pine scale	16	E	<i>Harmonia yedoensis</i> in Japan
11. elongate hemlock scale	19	E	explore Japan and China for parasitoids with better synchrony
12. oystershell scale	20	E	explore Russian Far East
13. San José scale	21	E	explore Russian Far East
14. Japanese beetle	32	E	explore China and Japan for better parasitoids
15. imported willow leaf beetle	33	E	explore China
16. elm leaf beetle	34	E	explore Europe and Asia
17. smaller European elm bark beetle	36	E	collect nematodes and microsporidia from Europe
18. black turpentine beetle	38	N	re-release <i>Rhizophagus grandis</i>
19. <i>Ips typographus</i>	41	E	collect in Europe, when needed
20. spruce budworm	42	N	collect in Europe and Japan from congeneric species
21. gypsy moth	51	E	explore Russia and China, but prepare detailed evaluation first
22. nun moth	52	E	collect in Europe, when needed
23. mimosa webworm	57	E	explore Asia and Australia
24. birch casebearer	58	E	explore Europe
25. larch casebearer	59	E	already controlled through natural enemy introductions
26. pine false webworm	63	E	compare status in Europe and North America
27. introduced pine sawfly	67	E	already controlled through natural enemy introductions
28. European spruce sawfly	68	E	already controlled through natural enemy introductions
29. larch sawfly	69	E	continue work in Europe on encapsulation-resistant parasitoids
30. European pine shoot moth	84	E	reassess pest levels in North America, then explore in Europe
31. Nantucket pine tip moth	85	N (but E in CA)	already controlled through natural enemy introductions
32. white pine weevil	88	N	collect in Europe from congeneric species
33. birch leafminer	93	E	collect in Europe

In some cases, these species have never been targets of natural enemy importations (e.g., beech scale, mimosa webworm, eastern spruce gall adelgid). In other cases they present opportunities for work additional to that done in the past. An example of the latter is searching new regions not considered or accessible in the past, for example the Caucasus Mountains, for predators of the balsam woolly adelgid.

Some species listed in this category have already been successfully controlled through natural enemy introductions (e.g., larch casebearer, European spruce sawfly, introduced pine sawfly, and Nantucket pine tip moth in California).

Most of the pests listed in this category invaded North America from other continents. A few, however, are native species (e.g., Cooley spruce gall adelgid, tuliptree aphid, Nantucket pine tip moth) that have invaded parts of the continent outside their historical ranges and become non-native pests in those locations.

For species that have invaded North America from abroad, it is important to identify the species' native homeland, which is not necessarily the area from which the pest came to North America. Many species, for example, appear to have moved from Russia or Asia to Europe and then to North America. In such cases, the species may lack important natural enemies in Europe as well as North America. Europe would thus be an inappropriate location in which to seek natural enemies able to suppress the pest.

A small number of native species have been considered as possible targets for natural enemy introductions, using species collected from European or Asian species related to the pest at the generic level. Examples include spruce budworm and white pine weevil.

Augmentation of natural enemies through artificial propagation and release

For pests of high-value sites (forest nurseries, shade trees, Christmas tree plantations), use of more expensive biological control products such as nematodes, predacious mites, or formulated pathogens is possible. Fourteen species were identified for which studies on the effectiveness of augmentative biological control seem useful (see Table 2, opposite).

Table 2. Species for which development of augmentative use of natural enemies is recommended			
Species	Pest Number	Pest Origin	Type of Natural Enemy
1. <i>Phyllophaga</i> spp.	28	N	nematodes & fungi
2. <i>Polyphylla variolosa</i>	29	N	nematodes & fungi
3. Black vine weevil	30	E	nematodes & fungi
4. strawberry root weevil	31	E	nematodes & fungi
5. Japanese beetle	32	E	nematodes & fungi
6. spruce budworm	42	N	<i>Bacillus thuringiensis</i>
7. Bruce spanworm	46	N	Nucleopolyhydrosis virus (NPV)
8. gypsy moth	51	E	<i>Bacillus thuringiensis</i> or NPV
9. red headed pine sawfly	64	N	NPV
10. Swaine jack pine sawfly	65	N	NPV
11. poplar borer	75	N	nematodes
12. cottonwood borer	76	N	nematodes
13. carpenterworm	81	N	nematodes
14. spruce mite	94	?	predaceous mites

Examples include the development of nematodes for the control of white grubs in forest nurseries, the use of *Bacillus thuringiensis* for control of defoliating Lepidoptera, and the use of nuclear polyhedrosis viruses for control of some species of sawflies.

**Studies of population dynamics to clarify importance of natural enemies
or identify modifications of silvicultural practices that enhance
effectiveness of existing natural enemies at production sites**

For some pests, insufficient information was found to judge the importance of natural enemies in the population dynamics of the species. In some cases there were needs to compare the importance of natural enemies between habitats (such as natural stands versus managed plantations) or locations (in North America versus the native range). A need for population dynamics studies of these sorts was identified for 17 species (see Table 3, next page).

Table 3. Species which need basic studies of their population dynamics to clarify reasons for typical population densities, or to determine if modifications of silvicultural practices can enhance natural enemy effectiveness

Species	Pest Number	Pest Origin	Aspect Needing Study
1. Saratoga spittle bug	22	N	effect of pipunculid parasitoids
2. cottonwood leaf beetle	23	N	population dynamics in natural stands vs. plantations
3. pine root collar weevil	25	N	population dynamics in natural stands vs. plantations
4. pine engraver	40	N	effect of slash management on natural enemies
5. jack pine budworm	43	N	effects of stand conditions on natural enemies
6. large aspen tortrix	44	N	basic population study
7. fall cankerworm	45	N	basic population study
8. Bruce spanworm	46	N	basic population study
9. spruce budmoth	55	N	basic population study
10. balsam gall midge	62	N	effects of Christmas tree plantation silvicultural practices on natural enemies
11. yellow-headed sawfly	70	N	comparison of natural enemies in open vs. shady sites
12. red oak borer	74	N	woodpecker conservation methods
13. European pine shoot moth	84	E	comparison of effects of stand age and vegetational diversity in Europe and North America
14. Nantucket pine tip moth	85	N	effect of vegetational diversity on natural enemies
15. eastern pine shoot borer	86	N	effect of vegetational diversity on natural enemies
16. cottonwood twig borer	87	N	importance of natural enemies in natural stands vs. plantations
17. larger pine shoot beetle	90	E	effects on natural enemies of slash management practices

Examples include the need to clarify the importance of pipunculid parasitoids attacking the Saratoga spittlebug, a need to study the effect of different slash management practices on natural enemies of pine engraver beetle and larger pine shoot beetle, and studies of effects of vegetation diversity on various shoot borers.

Situations in which there is no role for biological control

For 29 species (see Table 4, opposite) no role for biological control was identified.

Table 4. Species for which no important role for biological control was identified

Species	Pest Number	Pest Origin
1. pear thrips	1	E
2. introduced basswood thrips	2	E
3. pine bark adelgid	7	N
4. pine leaf adelgid	8	N
5. white pine aphid	9	N
6. woolly elm aphid	10	N
7. pales weevil	24	N
8. pitch-eating weevil	27	N
9. native elm bark beetle	35	N
10. spruce beetle	37	N
11. eastern larch beetle	39	N
12. spring cankerworm	47	N
13. forest tent caterpillar	49	N
14. eastern tent caterpillar	50	N
15. pine webworm	53	N
16. Zimmerman pine moth	54	N
17. bagworm	56	N
18. oak leafroller	60	N
19. saddled prominent	61	N
20. Virginia pine sawfly	66	N
21. two-lined chestnut borer	72	N
22. bronze birch borer	73	N
23. flatheaded apple borer	77	N
24. locust borer	78	N
25. white oak borer	79	N
26. whitespotted sawyer	80	N
27. banded ash clearwing	82	N
28. Columbina timber beetle	83	N
29. northern pine weevil	89	N
30. white cone beetle	91	N
31. arborvitae leafminer	92	N

These species were predominantly native (27) insects, for which natural enemy introductions were not likely to be relevant, and for which augmentative biological control methods were too expensive in view of the nature and distribution of the damage. While natural control by unmanipulated natural enemies is undoubtedly a factor to some degree in the population dynamics of these species, opportunities to intentionally employ silvicultural practices to increase biological control were not identified.

Exotic Plants and Biocontrol

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The region included in the Southern Appalachian Man and Biosphere (SAMAB) Reserve is an important center of plant diversity. It is also a highly scenic area, important to tourism. Other segments of the regional economy, including timber production and the reservoirs, are also tied to the health of the forests.

Unfortunately, the forests of the SAMAB region have been hard hit by a variety of invasive alien species, a kind of biological pollution. These species range across the taxonomic spectrum, from European wild boars to the chestnut blight. Other participants in the conference will provide updates on the pathogens and insects attacking trees native to the area. Dr. Randy Westbrooks and I will focus on the alien plant species that have invaded forests.

Review of a list of "worst" invasive plants for continental North America compiled from nearly 30 sources resulted in a list of 57 plant species that probably are important invaders in the SAMAB region. These include such familiar species as crown vetch (*Coronilla varia*), purple loosestrife (*Lythrum salicaria*), English ivy (*Hedera helix*), privet (*Ligustrum* spp.), autumn olive (*Elaeagnus umbellata*), and empress tree (*Paulownia tomentosa*).

Another hundred species may pose a threat to biological integrity of the region.

Invading alien plant species are not widely recognized as serious threats in the SAMAB region. I suggest that this lack of attention—dangerous, in my view—stems from the following factors:

1. These plant invaders cause less conspicuous ecosystem changes than situations such as that in Everglades National Park, where the melaleuca tree is replacing sawgrass. In the SAMAB region we have invading plants that are of similar structure to the natives they replace. In other words, shrubs are replacing shrubs—or sometimes creating a shrub layer where none previously existed. Trees are replacing trees, herbaceous understory plants replacing native wildflowers. The exotic vines are the most conspicuous, but even they somehow escape the notice of many.
2. Fewer drastic ecosystem changes are caused by invading alien plant species in the SAMAB region than are caused by similar invasions in some other ecosystems. For example, many of the invaders in

Hawai'i are changing local soil chemistry. In both Hawai'i and the Intermountain West, alien grasses are fueling much larger fires than in the past. These fires impinge on human activities and therefore command considerable attention. (Unfortunately, the role of exotics in fueling such fires is often not acknowledged at the time of crisis.)

3. We are unable to show that invading plants harm some vertebrate species. In fact, many of these plants have been promoted on the basis that their fruits are wildlife food.
4. The region's economic interests are not harmed as directly by these invading species as are those of other regions. For example, the interests of livestock ranchers are harmed by invasions of unpalatable leafy spurge, knapweeds, and yellow starthistle on the Great Plains and farther west.

This lack of economic links is not absolute in the SAMAB region. Farmers and utility operators hate several of the thistles and kudzu. However, in most cases, economic interests favor the invasive species: between 80% and 100% of the plant species listed in this study are promoted in the nursery trade.

What is being done to counter the most damaging of these invasive alien plant species? For the past three years, Great Smoky Mountains National Park has been carrying out a control or eradication program against 33 exotic plant species. This work has been funded by a grant under the Natural Resources Protection Program (NRPP). The assumption was that this expanded eradication effort would sufficiently reduce the weed species' range and density so that future control work could be carried out under the Park's normal budget for resource management. Now that the program is coming to an end, what is the prospect for such a resolution?

Chemical, mechanical, and muscle-powered control efforts are expensive, particularly in terms of time and person-power. Furthermore, they do little to prevent reinfection from seed sources outside the cleared area. (Here we see the true danger of those species promoted as food for wildlife.) For these reasons, biocontrol appears attractive.

Unfortunately, complications arise with regard to this approach, too. Because they have close relatives in North America, such damaging invaders as the honeysuckles, bittersweet, and *Ampelopsis*, regrettably, are unlikely to be suitable for biocontrol. Privets are major invaders in Great Smoky Mountains National Park, and indeed, throughout eastern deciduous forests. However, they are mainstays of the nursery trade; such an effort is virtually certain to meet with objections from that industry.

On a more hopeful note, Bernd Blossey of Cornell University is interested in pursuing biocontrols for one of the most troublesome of the ground-level herbs, garlic mustard (*Alliaria petiolata*; = *A. officinalis*).

Others are exploring the idea of a program aimed at tearthumb or mile-a-minute vine (*Tracaulaon [Polygonum] perfoliatum*), a species causing trouble in the Mid-Atlantic region that may spread to this area. Scientists need to discuss priority species for an expanded biocontrol effort aimed at pest plants of the eastern deciduous forests.

Finally, all involved with research and management in the SAMAB region should increase their efforts to inform their agencies, Congress, the media, and the public about the damage being caused by biological pollution and the options for combating these threats.

Biological Approaches to Chestnut Blight Control

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At the turn of the 20th century, the American chestnut tree was an integral part of the heritage of eastern North America. Chestnut wood played an important role in almost everyone's life from the time they were rocked in chestnut cradles until they were buried in chestnut coffins. More than one-fourth of all the hardwood timber cut in the Appalachians was chestnut. The tree was known for its straight bole, highly durable wood, and sweet flavorful nut. The chestnut grew from southern Maine and Ontario to northern Georgia and Alabama. Chestnut was the backbone of the forest economy in the Appalachians; no other species exceeded the volume of chestnut wood cut. Sale of nuts contributed significantly to many local economies, and extracts of tannins from chestnut bark kept numerous leather tanneries in business.

The American chestnut was destroyed in about 50 years by *Cryphonectria parasitica*, a fungus introduced from the Orient and discovered in New York City in the early 1900s. This fungus initiated one of the greatest natural disasters in the annals of forest biology. Despite early attempts at control, the fungus spread in ever increasing waves of approximately 25 miles per year from the leading edge. Local spread occurred as a result of wound infections initiated by wind- and rain-disseminated spores, but longer distance dispersal probably occurred via birds or through the movement of infected wood. Fortunately, chestnut has survived, principally as shoots produced from living root systems that continue to sprout. Unfortunately, these shoots become infected when they are one to 12 years old, perpetuating the cycle of blight.

As the disease progressed unabated in North America, efforts shifted to the only hope for control, breeding blight-resistant chestnut trees. Early breeding programs were designed to preserve the best traits of the American chestnut while incorporating resistant germplasm from the Chinese or Japanese chestnut. This approach relied almost entirely on making large numbers of crosses. Few second-generation trees were grown from first generation hybrids, and most F1 hybrids were backcrossed to a resistant parent, typically one that lacked the desired traits of the American chestnut. These undertakings met with limited success and were never designed to return the American chestnut to the forests of eastern North America.

Currently, two avenues of control are being pursued; both can be considered biological. The first approach, like earlier efforts, involves traditional plant breeding. Renewed interest in breeding blight-resistant trees came more than ten years ago with the realization that earlier breeding efforts had been haphazard. The current breeding program tests the hypothesis that the well established backcross plant breeding method is valid for chestnut. With this method, American chestnuts that are blight susceptible are crossed with resistant species. The first-generation hybrids then are backcrossed to American chestnut rather than to the resistant parent. Resistant plants are then selected by screening the backcross progeny. Further backcrosses to American chestnut are made with progeny that express high levels of resistance. With this approach, it should be possible to develop genotypically American trees that contain the resistance genes of the Asian species. Molecular biological studies also are underway to aid in the early identification of progeny that carry the appropriate genes for resistance. The breeding effort is being sponsored by The American Chestnut Foundation, a privately funded, non-profit organization whose goal is the restoration of the American chestnut.

A second approach to disease control became possible when Italian and French scientists observed non-lethal chestnut blight cankers on European chestnut growing in Italy. They observed that strains of the fungus associated with such infections produced colonies that were abnormally pigmented and shaped. They further demonstrated that these strains contained some "contagious factor" that was responsible for their inability to produce lethal infections. We now know that the factor responsible for the debilitation represents a new class of viruses called "hypoviruses". Other hypoviruses have since been found associated with *C. parasitica*. Researchers working with chestnut blight in North America were particularly encouraged when hypovirus-infected strains were found in stands of American chestnut recovering from blight in Michigan.

With the discovery of hypoviruses comes renewed hope that biological control of chestnut blight may be possible within the natural range of chestnut. Yet, major obstacles appear to limit the potential of hypoviruses. In areas where hypoviruses have effectively controlled *C. parasitica*, strains often are compatible with each other. Laboratory and field tests have revealed the presence of many genetically different strains of *C. parasitica* that are incompatible with one another in the Appalachians. When strains are incompatible, their hyphal filaments often fail to fuse, which prevents hypovirus transmission.

The task, then, is to devise methods that will allow us to bridge this system of incompatibility. Two approaches currently are being investigated. The first requires knowledge of the genetics of the compatibility system. We now know that some strains are inherently better transmitters of hypovirus than others. We believe that by understanding the genes that regulate compatibility, strains can be chosen for hypovirus

introduction that are more capable of interacting with large numbers of compatibility types.

A second approach has employed molecular biology techniques to integrate the hypovirus into the nucleus of *C. parasitica* (most naturally occurring hypoviruses are carried cytoplasmically). Nuclear integration provides an important gain for the hypovirus, as it allows transmission to occur during sexual reproduction. The barriers of incompatibility do not exist during sexual reproduction; therefore, when normal strains mate with those carrying hypoviruses, about one-half of the wind-borne sexual spores that are produced carry hypovirus. A further advantage of nuclear integration is that the hypoviruses are passed to a variety of compatibility types, a step that should further aid their distribution to the numerous existing strains.

Ultimately, the answer to chestnut blight control may rest with a marriage of biological control technologies. Because no species has adequately filled the niche once held by the American chestnut, its return would improve the balance of many eastern forest ecosystems.

Suggested Readings

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Potential for Biologically Based Control of Beech Bark Disease in the Southern Appalachians

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Abstract

Beech bark disease results when the bark of *Fagus* spp. is altered by the beech scale *Cryptococcus fagisuga* and then invaded and killed by fungi of the genus *Nectria*. Biologically based factors or agents are potentially useful for controlling both members of the causal complex. On several sites in Nova Scotia, bark epiphytes (lichens) provide significant levels of protection against the insect. Also, several invertebrate predators are effective in reducing scale populations on individual trees, though they offer little promise for control at the stand level. The effects of the entomogenous fungus, *Verticillium lecanii*, found associated with collapsed scale populations in England, have not been studied in North America. Although *Nectria* spp. are parasitized by the mycoparasite *Nematogonium ferrugineum*, and other fungi are suspected competitors or antagonists, control of the *Nectria* pathogens offers less potential for controlling the disease than factors and agents that affect *C. fagisuga*. Most important is that some American beech trees are resistant to the scale. Resistance offers the greatest opportunity for exploitation at this time.



Figure 1. Beech scale nymph (about 0.3 mm long).

Introduction

In North America, beech bark disease (BBD) is a complex affecting American beech (*F. grandifolia* Ehrh.). Its etiology includes the predisposing attack of bark by the beech scale insect, *Cryptococcus fagisuga* Lind. (see Figure 1) and subsequent invasions and killing of infested bark by several fungi of the genus *Nectria* (Ehrlich 1934).

The principal fungus is *N. coccinea* var. *faginata* Lohm. and Watson (Lohman and Watson 1943) (see Figure 2), though *N. galligena* Bres. also attacks and kills bark predisposed by *C. fagisuga* (Cotter 1974; Houston 1994a; Mielke et al. 1982).

A general framework for the etiology of BBD can be expressed as:

Beech trees + *C. fagisuga* + *Nectria* spp. => BBD

This framework correctly implies that a specific chronology of events is required for disease development, and that while the effects of the insect are necessary for the disease to develop, the disease is expressed only when *Nectria* spp. attack scale-altered tissues. Conversely, *Nectria* attack does not occur unless trees are infested by beech scale.

Brought to Nova Scotia accidentally around 1890 (Ehrlich 1934), *C. fagisuga* has steadily spread westward and southward through the natural forests of Canada and the United States (see Figure 3).



Figure 2. Sexual fruiting bodies (perithecia) of *N. coccinea* var. *faginata* (about 0.3 mm in diameter)



Figure 3. Known distribution of beech scale (black areas) as of 1996 in relation to the range of American beech (gray areas).

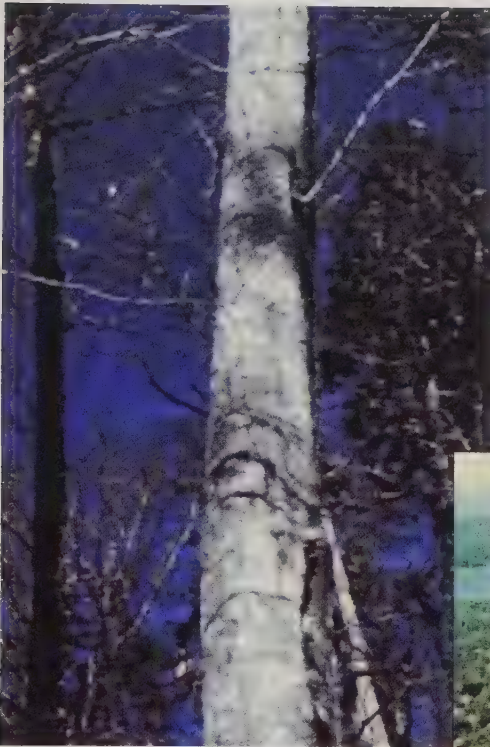


Figure 4. Heavy infestations of beech scale can cover tree boles with white wax.



Figure 5. Tree mortality (trees with bare and discolored crowns) can be high when forests are affected by the causal complex for the first time.

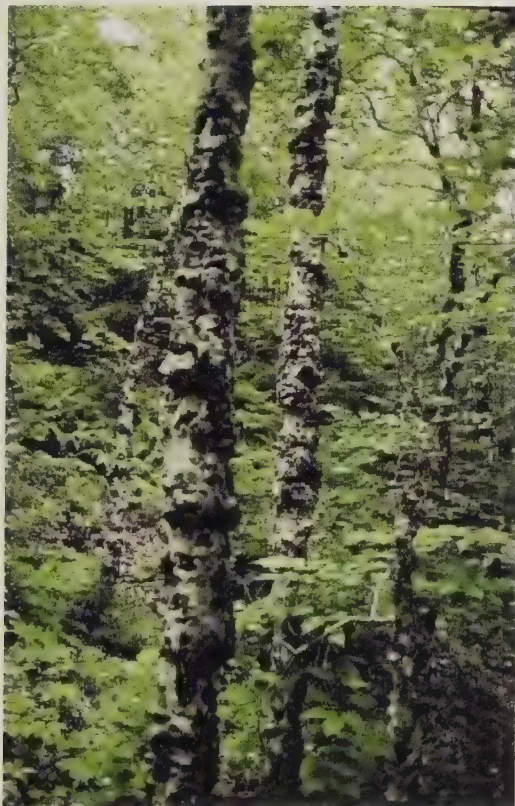


Figure 6. Trees in aftermath forests can become severely defective as cankers accumulate over time.

C. fagisuga now is found throughout New England, New York, much of Pennsylvania, northeastern Ohio, northeastern West Virginia, northwestern Virginia, and in a small area of the Great Smokey Mountain National Park on the Tennessee-North Carolina border (Houston 1994 a, b). Generally, *Nectria* infections and tree mortality occur one to four years following a heavy buildup of the insect on large trees (see Figure 4).

The area of current heavy mortality is termed the "killing front" (see Figure 5).

Regions in which severe mortality has occurred earlier comprise the "aftermath zone" (Shigo 1972). In aftermath forests, causal agents are established on small trees of root sprout and seedling origin that often develop in dense stands. Most of both the new emerging trees and the old survivors become cankered and are rendered highly defective by the scale-*Nectria* complex (see Figure 6).

Biological Factors and Agents Affecting *C. fagisuga*

Four biological factors and agents affect *C. fagisuga*: host resistance, bark epiphytes, predators and parasites, and microbial pathogens.

Host Resistance

In affected stands, some trees remain free of beech scale and disease (see Figure 7).

Challenge trials have shown them to be resistant to *C. fagisuga* (Houston 1982, 1983a). Resistant trees are found in relatively low numbers (< 1 percent of the beech stems) and commonly occur in groups (Houston 1983a). That resistant trees occur in groups is encouraging, because this makes them easier to recognize than isolated individuals; they are thus potentially easier to protect in forest management operations designed to discriminate against diseased trees. Isozyme genetic studies have shown that groups of resistant trees originate both from root sprouts and seed (Houston and Houston 1986, 1990).

Increasing the relative number of resistant trees is important in reducing the impact of BBD. Researchers are analyzing the results of trials to determine the effects of various harvesting regimes on the initiation, development, and survival of root sprouts. In addition, studies to determine how to clone selected resistant genotypes have been conducted. Tissue-culture techniques in which sprouts from root segments and forced buds of mature resistant trees are used have brought several genotypes through to rooting (Barker et al. 1995). Still needed are trials to develop ways to grow the tissue-culture plantlets in soil and introduce them into the forest.



Figure 7. Some trees are resistant to beech scale and remain free of disease (right) in contrast to their susceptible neighbors (left).

Bark epiphytes

Some epiphytes growing on beech bark offer favorable spatial habitats for *C. fagisuga* (Ehrlich 1934; Houston et al. 1979). Infestations often develop initially beneath patches of moss and lichen. However, not all epiphytes enhance infestations. In Europe, the common bark fungus *Ascodichaena rugosa* sometimes produces a dense, relatively continuous stromatic layer on European beech, *F. sylvatica* L. (Butin 1977); as a consequence, *C. fagisuga* often is absent on densely infected bark (Houston et al. 1979). However, trials initiated in 1975 revealed that although infestation by *C. fagisuga* of bark infected by *A. rugosa* remained low, stromatic patches sometimes were not sufficiently dense or complete to preclude significant infestation and subsequent development of BBD (D. Lonsdale, pers. commun.). In North America, stromatic patches of *A. rugosa* often are thin and fractured; thus they can offer refuges for *C. fagisuga*—sometimes on trees too small to be infested otherwise (pers. observation).

In Nova Scotia, some stands on steep, south-facing slopes contain many beech trees that are remarkably free of disease compared to others in the general area. These trees are heavily colonized by mosaics of crustose lichens. Several of the predominant lichen species are rarely colonized by *C. fagisuga* (Houston 1983b). Such lichens have thalli that are dense, smooth, and epigenous in contrast to the loosely compact, granular-surfaced hypogenous thalli of readily colonized species.

Predators and parasites

To date, no invertebrate parasites of *C. fagisuga* have been found, but several predators are known. In North America, *Chilocorus stigma* Say. is the most common predator. *C. stigma* is most abundant when scale populations are dense. Although it responds numerically to high scale densities, its predatory effectiveness is limited by its propensity to disperse, by its failure to feed on all life stages of scale, and especially by the high rate of scale reproduction (Mayer and Allen 1983). Although scale populations on individual trees have been markedly reduced when populations of coccinellids were high, the overall effectiveness of this predator in controlling beech scale is limited.

Microbial pathogens

In North America today, scale populations are low in some stands and regions where they were once high. In some forests, we have observed precipitous and unexplained population declines of scale. Similar crashes in other forest insect populations have been associated with attacks by microbial pathogens.

In England, the entomogenous fungus *Verticillium lecanii* Viegas was common where infestations of beech scale were or had been heavy (Lonsdale 1983). The presence of *V. lecanii* depended on high scale density or on coalescence of scale colonies. It was absent from small, isolated, or new scale colonies because it spreads from one colony to another by hyphal growth rather than by aerially dispersed spores (Lonsdale 1983). We do not know whether *V. lecanii* or another pathogen is responsible in North America for observed sharp declines in scale populations or the maintenance of collapsed populations at low levels.

Agents Affecting *Nectria* spp.

Mycoparasites

Nematogonum ferrugineum (Pers.) Hughes (*Gonatorrhodiella highlei*) is a biotrophic contact mycoparasite (Barnett and Binder 1973) that obtains its nutrients from the living cells of its host. The first association of the fungus with BBD was in North America (Ayers 1941). *N. ferrugineum* also was commonly associated with *N. galligena* both on cankers of several hardwood species and on beech with BBD (Houston 1983c; Mielke and Houston 1983). The effects of parasitism by *N. ferrugineum* in nature are not known even though high populations of the fungus sometimes occur after severe outbreaks of BBD.

In culture, growth of parasitized *Nectria* spp. is little affected (Blyth 1949; Gain and Barnett 1970); though production of conidial and perithecial initials is reduced (Shigo 1964). In inoculation trials, parasitized isolates of *N. coccinea* var. *faginata* and *N. galligena* spread more slowly in bark and cambial tissues and persisted for shorter periods in bark tissues than did unparasitized isolates. Although cankers resulting from parasitized *N. coccinea* var. *faginata* isolates produced fewer perithecia (Houston 1983c), this fungus appears ineffective as a biocontrol agent because in nature it becomes abundant only following severe outbreaks of BBD.

Biological Control: Discussion and Conclusions

The beech scale is now well distributed throughout the Great Smoky National Park (K. Johnson, pers. commun.), and BBD is causing significant mortality in upper elevation beech gap stands. While this situation creates a sense of urgency, it also offers the opportunity to exploit what we have learned about the disease in other areas.

BBD is complex because of its dual organism etiology. While this duality might seem to offer added opportunities for biological control, earlier studies indicate that approaches focused on reducing the effects of the scale initiator hold the most promise. The following actions seem feasible at this time:

1. Areas in the Southern Appalachians now severely affected by BBD should be searched for trees exhibiting resistance to the beech scale. Identified trees will serve as candidates for future cloning and reintroduction into severely impacted forests.
2. Tissue-culture techniques designed to preserve and increase the relative numbers of resistant individuals and clones need to be improved, and steps toward transferring plantlets from tissue-culture media to soil and establish them in forest settings need to be developed.
3. Potential sites on which beech can be grown and protected from beech scale by lichens should be identified.
4. Western Europe may not be the site of origin of *C. fagisuga*. Should its true home range be identified elsewhere, a search should be made there for pathogens, parasites, or predators.

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Butternut Canker

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Abstract

Butternut canker, caused by the fungus *Sirococcus clavigignenti-juglandacearum*, is killing butternut (*Juglans cinerea*) throughout its range in North America. First reported from Wisconsin in 1967, the disease has killed up to 80 percent of the butternut in some states. The primary hope for biological control rests with genetic selections. Healthy trees, and infected trees that apparently have resistance and have survived the disease, have been found in severely affected forest stands in 19 states. Clonal and seedling propagation of trees exhibiting resistance is being used to evaluate breeding and future restoration efforts. Hybrids are also being evaluated as an alternative biological control technique. A number of trees have been observed recovering from butternut canker. This pattern of major loss of trees followed by recovery of the remaining trees is typical of hypovirulent fungal strains and needs exploration.

Butternut (also called White Walnut and oilnut) is a small-to-medium size tree that matures at about 75 years of age, is shade intolerant, and reproduces by either sprouting or seed germination. It grows on rich, loamy soils, as well as drier, rocky soils. Butternut typically is mixed with other hardwoods such as black walnut. The species is found in New England, south to Northern Georgia, in the United States from west to central Missouri and north to the Lake States (Distribution Map). It hybridizes with other species of *Juglans* such as heartnut, Japanese walnut, English Walnut, little walnut, and Manchurian walnut.

Butternut is valued for its wood for furniture, paneling, specialty products, carving, and nut production. It is second in value only to black walnut. Although walnut is not commonly found growing together in great numbers, there is concern to maintain a viable butternut population to preserve biodiversity.

The Disease

Butternut is being killed throughout its range in North America by the fungus (*Sirococcus clavigignenti-juglandacearum*) which causes butternut canker. Butternut canker has been found in 55 counties in the southern United States (Occurrence Map). Numbers of butternut trees have been dramatically reduced; butternut has been placed in Category 2 on the list of Endangered and Threatened Plants under the Endangered Species Act. Placement in this category implies that there is some evidence of vulnerability, but not enough data to support listing as an endangered species at this time.

The canker was first reported on butternut in southwestern Wisconsin in 1967. Detailed examination of cankers indicates that butternut canker has been present in the United States since the early 1960s, but it was not until 1979 that the true cause of butternut canker was identified. The origin of the fungus is unknown, but the evidence points to this being a recent introduction. The rapid spread of the fungus throughout the butternut range, the highly aggressive nature of the disease on infected trees, the scarcity of resistant trees, the lack of genetic diversity in the fungus, and the age of the oldest cankers (50 years) all support the theory of a recent introduction.

Symptoms

The fungus causes multiple cankers on the main stem and branches of butternut trees. Young cankers are elongated, sunken areas, commonly originating at leaf scars and buds, often having an inky black center and whitish margin. Peeling the bark away reveals brown-to-black elliptical areas of killed cambium. Older branch and stem cankers are perennial, found in bark fissures or covered by shredded bark, and bordered by successive callus layers. Cankers commonly occur at the bases of trees and on exposed roots. Branch cankers usually occur first in the lower crown; stem cankers develop later from spores washing down from branch cankers. The fungus can survive and sporulate on dead trees for at least 20 months.

Spores of the fungus are disseminated from fruiting bodies by rain splash and possibly by insects. Spores are produced throughout the growing season and, once airborne, can survive and be dispersed long distances during favorable weather conditions (cool temperatures and overcast skies).

Impact

Butternut canker kills trees of all ages. Branches and young saplings may be killed by a single canker; however, older trees are killed by multiple, coalescing cankers that either progressively kill the crown or eventually girdle the stem. Sprouts, if they develop, also become infected and usually are killed within the first few years. The nut husk can also become infected.

USDA Forest Service Inventory and Analysis forest inventory data show a dramatic decrease in the number of live butternut trees in the United States. Live butternut decreased by 58 percent in Wisconsin and 84 percent in Michigan in the last 15 years. A recent Wisconsin Department of Natural Resources survey revealed that 91 percent of the live butternut throughout Wisconsin were diseased. Surveys in the south-east United States revealed that 77 percent of butternut trees have been killed in North Carolina and Virginia. Infected trees continue to be found in new counties throughout its range.

Biological Control Potentials

There is no known control for butternut canker. Fungicides have been tested with some success, but they are not ready for field use. No agents which would be antagonistic to the fungus, such as hypovirulent fungal strains, have been detected. However, a number of trees have been observed recovering from butternut canker. This pattern of major loss of trees followed by recovery of the remaining trees is typical of hypovirulent fungal strains and needs exploration.

The fungus is not known to occur in other countries, so the potential for finding a biological control from another geographic area is limited. The primary potential for biological control of the butternut canker is through genetics.

Disease-free trees are rare, but they have been found in 19 states. These trees are growing along side severely cankered trees. The rapid spread of the fungus in addition to their proximity to diseased trees, indicates that these trees have received prolonged exposure to the fungus. Each disease-free tree discovered is tagged and placed into a superior tree selection program. Scion wood is collected from each of these disease-free trees in February and March. The scion wood is grafted on root stock at the University of Tennessee and at the North Central Forest Experiment Station in St. Paul, Minnesota. Nuts from disease-free trees are also collected, when available, and seedlings are grown in a nursery.

These grafted and seedling tree selections are placed into progeny tests and evaluated for growth traits. They are screened for relative resistance and placed in seed orchards for future use. It is too early to evaluate the success of selecting for disease resistance, but the preliminary data is promising.

Butternut also hybridizes with trees such as heartnut. Some of these hybrids have been located in the field and are being evaluated. These trees provide the potential for using back crosses to produce progeny which contain a small amount of heartnut but are resistant to the fungus.

Retaining Trees for Genetic Selections

The need for the identification and conservation of butternut for tree selection and breeding was recognized in the late 1980s. The following guidelines were prepared:

1. Retain trees with more than 70 percent live crown and with less than 20 percent of the combined circumference of the stem and root flares affected by cankers.
2. Harvest dead or declining trees to salvage the quality and value of the wood, or maintain the trees in the forest for their wildlife value.
3. Retain trees free of cankers with at least 50 percent live crown which are growing among diseased trees. These trees may be resistant and therefore have potential for propagation by grafting or future breeding.

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Biological Control of the Gypsy Moth: An Overview

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Biological control is the regulation by natural enemies (pathogens, parasites and predators) of an organism's population at a lower density than would otherwise occur. Biological control can occur spontaneously due to native natural enemies; it can be applied by people; or can occur fortuitously, that is, caused by the accidental introduction of natural enemies.

Most biological control of the introduced gypsy moth, *Lymantria dispar* (L.), in the United States has been applied, following a classical approach using parasites. This approach involves searching for parasites in native habitats of the gypsy moth, importing them, and releasing them in the hope that they will become established in this country and exert biological control on gypsy moth populations. The use of augmentation, which is the manipulation of natural enemies by people for more immediate control, against the gypsy moth has been minimal.

This paper provides background material on the gypsy moth and describes the effect of pathogens, parasites, and predators on gypsy moth populations.

About the Gypsy Moth

The gypsy moth caterpillar is a serious defoliator of broadleaved forests in eastern North America. In addition, this pest defoliates trees and shrubs in residential areas, causing economic and aesthetic impacts, and, when infestations are heavy, creating a nuisance to residents. Caterpillars prefer hardwoods but may feed on several hundred different species of trees and shrubs. During periods when gypsy moth populations are dense, larvae feed on almost all vegetation. Trees weakened by consecutive defoliation are vulnerable to attack by disease organisms and other insects. For example, the *Armillaria* fungus

attacks the roots of weakened trees, and the two-lined chestnut borer attacks the trunk and branches.

Life Cycle

The gypsy moth has one generation per year, passing through four life stages: egg, caterpillar, pupa, and adult (moth stage). Only caterpillars which reach maturity between mid-June and early July defoliate trees and shrubs. After six to eight weeks, caterpillars enter the pupal stage for seven to 14 days, which changes them into adults (moths). Flightless female moths mate and lay their eggs in masses in July and August. Four to six weeks later, embryos develop into caterpillars. The caterpillar embryos remain in the eggs during the winter and emerge from the eggs the following spring, coinciding with the budding of most broadleaved trees (McManus et al. 1989).

Distribution

The gypsy moth is not native to North America; it was introduced from Europe in 1869 near Boston, Massachusetts. Historically, populations of the gypsy moth have undergone periodic outbreaks, reaching extremely high densities that resulted in widespread defoliation to an average of 3.0 million forested acres per year. More recently (1992 through 1996), populations have been declining, with an average of 1.0 million forested acres per year being defoliated. This decline is partly due to the rapid spread of an introduced fungus (see Figure 1).

Since the introduction of the European or North American strain of gypsy moth, it has spread south and west, and continues to spread along the leading edge of infestation at the rate of approximately 12 miles per year (see Figure 2, opposite). The Asian strain of gypsy moth, recently introduced on the East and West coasts of North America, has been eradicated.

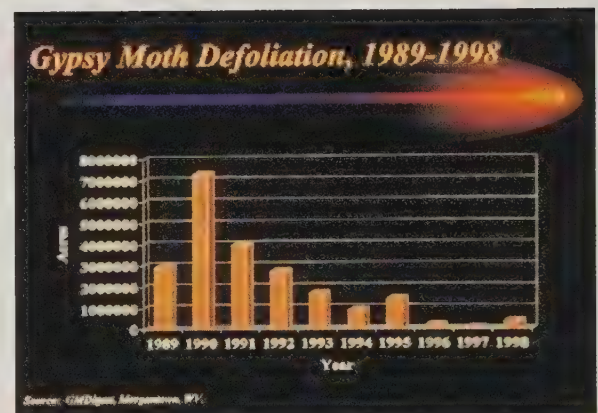
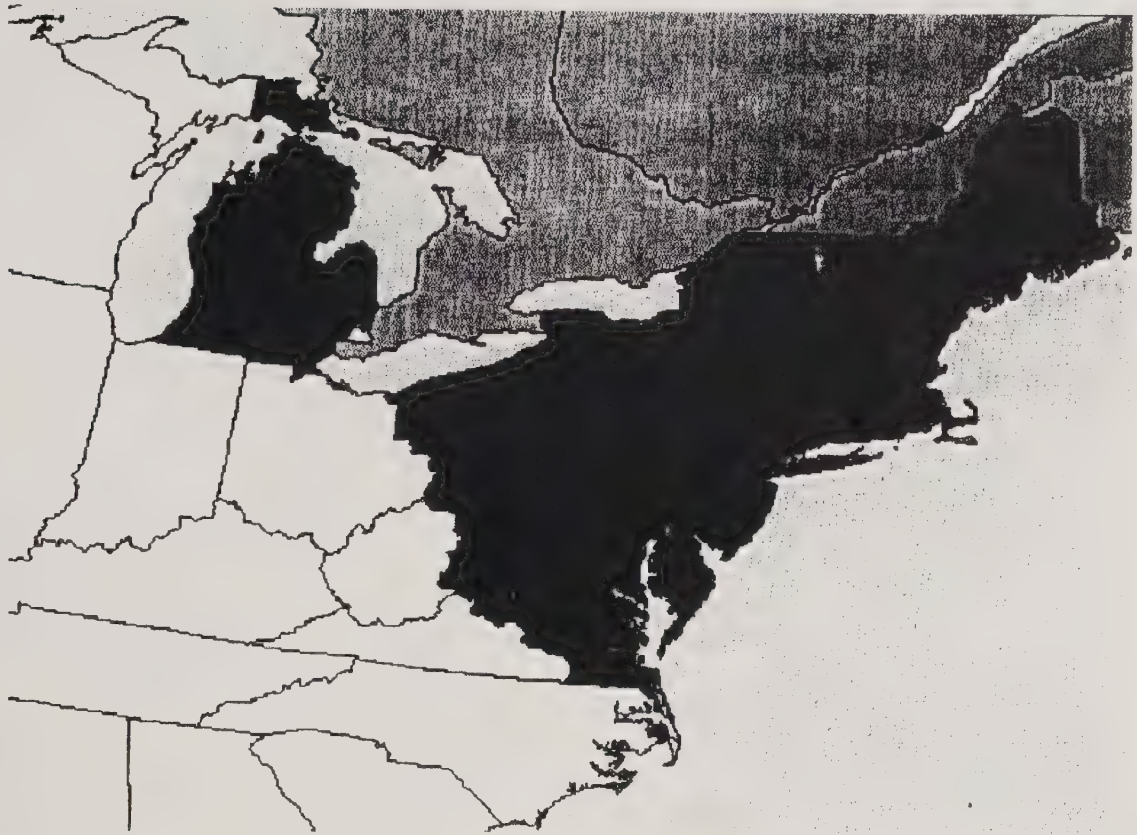


Figure 1. Acres of gypsy moth defoliation by year in the United States.

Figure 2.
Distribution of
the gypsy moth
in North
America in
1996.



Biological Control of the Gypsy Moth: Pathogens

In eastern North America, the gypsy moth is subject to a variety of naturally occurring infectious diseases caused by several kinds of pathogens: bacteria, fungi, and a nucleopolyhedrosis virus (NPV). The NPV, which was inadvertently introduced either with the gypsy moth or with its parasites, and an introduced fungus, *Entomophaga maimaiga*, cause widespread mortality and are described here. The other pathogens cause only limited mortality and are not described here.

Virus



Figure 3. Gypsy moth caterpillars killed by the nucleopolyhedrosis virus.

The naturally occurring disease caused by the NPV is often referred to as "wilt" due to the soft, limp appearance of the diseased larvae (see Figure 3). The disease can reach outbreak (epizootic) proportions as gypsy moth population densities increase. These outbreaks result from increased transmission rates within and between generations of the gypsy moth, as small caterpillars become infected and die on leaves in the crowns of trees. When these

caterpillar cadavers disintegrate they serve as inocula for healthy feeding caterpillars.

Also, virus transmission occurs when adult females deposit their egg masses on NPV-contaminated surfaces. Caterpillars hatching from these contaminated eggs in the following spring have a high risk of contracting the disease. Birds and mammals have the ability to pass and disperse active gypsy moth NPV. Parasites and invertebrate predators may also play a role in the transmission of gypsy moth NPV within natural populations.

In many dense gypsy moth populations, the virus kills up to 95% of the larvae and reduces populations to levels where they cause only minimal defoliation and tree damage in the following year (Reardon et al. 1996).

In the late 1950s, the USDA Forest Service began to explore the feasibility of developing NPV as an alternative to chemical insecticides for suppressing gypsy moth populations. In April 1978, the gypsy moth nucleopolyhedrosis virus product Gypchek was registered for use by the Environmental Protection Agency (US EPA). Today, Gypchek is produced in live gypsy moth caterpillars in the laboratory by the USDA Forest Service and the USDA Animal and Plant Health Inspection Service (APHIS), processed, and made available for aerial and ground application as part of the Federal and State Cooperative Suppression Program.

Fungus

In 1908, pest managers in the Boston area introduced the fungus *Entomophaga maimaiga* via infected gypsy moth larvae collected in Japan. Releases continued until 1911, when the local gypsy moth populations collapsed and there was no longer a way to continue propagating the fungus. In June and July 1989, *E. maimaiga* was recovered in North American gypsy moth and was found to be causing extensive epizootics in populations of gypsy moth in seven contiguous northeastern States (Connecticut, Massachusetts, Vermont, New Hampshire, New Jersey, New York and Pennsylvania). By 1990, the fungus was also recovered in three more northeastern states (Maine, Delaware, Maryland) and in southern Ontario. Today *E. maimaiga* occurs in most areas where the gypsy moth occurs and is prevalent in low-to-high density gypsy moth populations, causing up to 95% mortality of large caterpillars (see Figure 4). The fungus is highly variable, and as yet unpredictable, in reducing gypsy moth populations. It is not applied as a direct control. Fungal resting spores in soil and infected gypsy moth cadavers are collected and dispersed by



Figure 5. Gypsy moth caterpillars killed by the fungus *Entomophaga maimaiga*.

hand to spread the fungus to new locations, although natural spread has been fairly rapid (Reardon and Hajek 1998).

Parasites

The use of parasites against the gypsy moth has been one of the most massive programs in biological control history (Reardon 1981).

1905 to 1980

From 1905 to 1980, approximately 78 species of parasites (over 200,000 individuals) were sent to the USDA Agricultural Research Service (ARS) quarantine facilities in the United States. Of these, approxi-

mately 53 species were shipped to cooperating agencies for initiation of laboratory colonies or release. Between 1905 and 1914, gypsy moth caterpillars and pupae containing parasites were collected in Europe, Japan, and Russia and shipped to the United States. Six of the parasite species imported and introduced became established. Parasite importation was reinstated in 1922 to 1933 along with searching for gypsy moth infestations in France, Spain, Italy, Germany and Japan. These efforts led to the establishment of two flies and the possible establishment of one wasp (see Table 1).

Gypsy moth life stage parasitized	Parasite species	Type of parasite	Imported and introduced
Egg	<i>Ooencyrtus kuvanae</i>	Wasp	1905-1914
	<i>Anastatus disparis</i>	Wasp	1905-1914
Caterpillar	<i>Cotesia melanoscela</i>	Wasp	1905-1914
	<i>Phobocampe uncinata</i>	Wasp	1905-1914
	<i>Aleiodes indiscretus</i>	Wasp	1996-1979
	<i>Compsilura concinnata</i>	Fly	1905-1914
	<i>Parasetigena silvestris</i>	Fly	1922-1933
	<i>Blepharipa pratensis</i>	Fly	1905-1914
Pupa	<i>Exorista larvarum</i>	Fly	1922-1933
	<i>Brachymeria intermedia</i>	Wasp	1922-1933
	<i>Coccygomimus disparis</i>	Wasp	1980-1992

During both periods of foreign exploration, 1905-1914 and 1922-1933, hosts and parasites were collected from high-density gypsy moth populations. Limited foreign exploration was resumed in the 1960s, and in the 1970s ARS established gypsy moth projects at their European Parasite Laboratory in France and Asian Parasite Laboratory in Japan. Only one exotic species of parasite was established during this period, probably because of numerous problems associated with rearing and releasing parasites. Problems with rearing include inadequate taxonomic identification and poor and variable host quality and quantity. Problems with releasing parasites include inadequate numbers, "laboratory" strains that were not adaptable to field conditions, lack of alternate or overwintering hosts, and lack of host density and habitat requirements.

One exotic species of parasite, released in the late 1960s and 1970s, was not recovered until 1996. Several parasites native to the United States have become opportunistic parasites of the gypsy moth; that is, they parasitize gypsy moths when they are available. The augmentation approach, either as inundative releases (in which released individuals regulate) or inoculative releases (in which progeny of released parasites regulate generations of the gypsy moth) has been attempted, with numerous species, against both artificial and natural gypsy moth populations. In general the incidence of parasitism by the released species increased, but no impact on gypsy moth populations was detected. Also, combinations of natural enemies (e.g., aerial application of the bacterial insecticide *Bt* and releases of *Cotesia melanoscela*, to transmit NPV) have been used with limited success.

1980 to 1992

Prospects for using both classical and augmentation approaches to improve biological control of the gypsy moth were explored again during the 1980s and early 1990s. Foreign exploration for parasites shifted to Asia, and 17 parasite species were received at ARS quarantine in the United States. Most of these (parasites of Indian gypsy moth, *Lymantria obfuscata* Walker) were from Korea, Japan, and India. Little material was obtained from the other promising regions, China and the Russian Far East. Releases of 15 species were made, but establishment of only one species, the pupal parasite *Coccygomimus disparis* (Viereck) was confirmed. This species appears to be dispersing well over the generally infested area, but with limited effectiveness against the gypsy moth, since it parasitizes numerous species.

1993 to 1997

Recent interest in the classical approach to biological control has been provided through the National Biological Control Institute (USDA APHIS) and "New Directions in Biological Control of the Gypsy Moth" with efforts focusing in non-outbreak sites on promising species that have not been previously introduced. Dominant species from southern Europe that failed to become established in New England or the Middle Atlantic States (e.g., *Glyptapanteles porthetriae* [Muesebeck]) are being imported and reared for release in the southern states with different forest habitat types, climate, and availability of alternate host species (Fuester 1993). Manipulative experiments conducted in New England suggest that artificial elevation of gypsy moth populations might be useful for maintaining populations of insects that parasitize caterpillars, such as *Compsilura concinnata* (Meigen), *Parasetigena silvestris* (Robineau-Desvoidy), and *Cotesia melanoscela* (Ratzeburg).

Predators

Many species of animals in the United States eat the gypsy moth and other defoliating insects. The gypsy moth predator community is complex; it includes about 50 species of birds and 20 species of mammals, along with some amphibians, reptiles, fish, insects, and spiders.



Figure 5. Adult stage of the carabid beetle *Calosoma sycophanta*.

Only a few of these predators are known to affect gypsy moth population dynamics. The predators are all opportunistic feeders, which means that their taste for the gypsy moth depends upon the scarcity of other preferred foods. Vertebrate predators, especially the white-footed mouse (*Peromyscus leucopus*), are major sources of large caterpillar and pupal mortality in low density gypsy moth populations. Recent studies of bird predation tend to show that gypsy moth is not a major food item of most species.

Insect predators, especially ants and the imported carabid beetle *Calosoma sycophanta* (see Figure 5), have a limited impact on gypsy moth populations. *Calosoma sycophanta* was imported from Europe between 1905 and 1910 and became established easily. It is common throughout most of New England and extends into New York, New Jersey, central Pennsylvania, and northeast Maryland. The beetle is a specific predator of gypsy moth; it is usually associated with high-density gypsy moth populations.

Conclusions

In general, parasites, together with other natural enemies (predators and pathogens) help regulate populations of the gypsy moth by reducing their numbers. Whether these introduced parasites have reduced the average population density of the pest or lengthened the periods between outbreaks is difficult to determine. The rate of parasitism from a particular parasite species varies from site to site and from year to year, depending on such factors as the number of gypsy moth larvae, the number of alternate hosts, and the weather.

Eleven exotic species of parasites have been established and continue to disperse along with the gypsy moth. Natural enemies are thought to help maintain low-density populations, but not to prevent the buildup of already increasing populations. Foreign exploration for natural enemies has occurred throughout most of the native range of the gypsy moth. In the continued search for biological control agents, selection of candidates focuses on species that are (1) from low-density gypsy moth populations, (2) limited to one generation per year, (3) new or not previously released, and (4) found to preferentially attack female gypsy moth caterpillars or pupae.

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Woolly Adelgids in the Southern Appalachians: Why they Are Harmful and Prospects for Control

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Abstract

The isolation of fir and hemlock in eastern North America coupled with the lack of native North American adelgids in the genus *Adelges* has resulted in these trees being vulnerable to adelgids introduced from other regions. The impact of the adelgids is exacerbated by the lack of natural enemies that could make a host shift from native species to the introduced species. The program to introduce natural enemies of *Adelges piceae* Ratzeburg and reasons for its failure are reviewed. The natural enemies of *Adelges tsugae* Annand found in Asia and recent efforts to introduce some of these are examined in the context of impacts on native fauna. Recommendations are given for the control of *A. piceae* on Fraser fir and *A. tsugae* on eastern hemlock.

Introduction

The Southern Appalachian region has two tree species found nowhere else: Fraser fir, *Abies fraseri*, and Carolina hemlock, *Tsuga carolinia*. These two species are isolated, ice-age relics closely related to the more widespread balsam fir, *Abies balsamea*, and eastern hemlock, *Tsuga canadensis*, respectively. Small, aphid-like sucking insects in the family Adelgidae are important pests of these four conifers. The firs are attacked by *Adelges piceae* Ratzeburg, the balsam woolly adelgid, and the hemlocks by *Adelges tsugae* Annand, the hemlock woolly adelgid. Both of these adelgids are non-native, exotic species accidentally introduced several decades ago.

Host Tolerance

Adelgids usually cause little harm to their hosts in most parts of the world. The damage done by adelgids to native firs and hemlocks in eastern North America is unusual. The following non-technical examination of the systematics and distribution of species in the family Adelgidae and some of their hosts is provided to show why fir and hemlocks in eastern North America are so vulnerable to adelgids.

Adelgidae and their distribution

Adelgids belong to a group in the super-family Aphidoidea, which is in the order Homoptera. The Aphidoidea includes the families Aphididae, Adelgidae, and Phylloxeridae. The members of these families are all small, soft-bodied, and feed on plant sap. The Adelgidae have the most limited host range, feeding exclusively on conifers. Unlike the true aphids, which produce live young and lay eggs, the adelgids only produce eggs. Parthenogenesis is a trait of adelgids that fosters rapid population increase.

The family Adelgidae is divided into two genera: *Adelges* and *Pineus*. All species of *Pineus* have a species of *Pinus* (pine) as a secondary host, except for *P. abientinus* Underwood and Balch, which is anholocyclic on *Abies* (fir). The *Adelges* have either *Abies*, *Pseudotsuga*, *Tsuga*, or *Larix* as secondary hosts. For both genera, the primary host is always a species of *Picea* (spruce). The basic life cycle lasts two years and has five different morphs with alternation between two host plants. Many adelgids can remain on the secondary host with only parthenogenic reproduction occurring. The lack of an obligatory migratory stage fosters the build-up of very large colonies.

There are about 30 species of *Adelges* worldwide (Blackman and Eastop 1994) but only six species occur in North America, and only one of the six appears to be native (there is some question whether three additional species that feed on larch in the West actually exist). *Adelges cooleyi* (Gillette) is the only distinct species in the genus *Adelges* that is clearly native to North America. It originally was found in western North America where *Pseudotsuga menziesii* (Douglas-fir) is the secondary host. It forms conspicuous galls on *Picea pungens* (blue spruce). The adelgid has spread to eastern North America and Europe, where these hosts have been widely planted.

There are about 20 species of the genus *Pineus* worldwide, and half of these can be found in North America (Blackman and Eastop 1994). Seven of these species appear to be native to North America and three of these, *Pineus strobi* (Hartig), *P. pinifoliae* (Fitch), and *P. floccus* (Patch), seem to be indigenous to eastern North America. These species attack eastern white pine, *Pinus strobus*, but seldom cause damage. These pine adelgids produce several overlapping generations on pine during the spring and summer (Raske and Hodson 1964). This contrasts with *Adelges* spp. that usually produce only two generations per year on the secondary host.

Distribution of fir and hemlock

There are some 40-odd species of *Abies* (true fir) worldwide; seven of these are native to western North America and two to eastern North America. There are no native adelgids that attack fir trees in North America. By contrast, Europe has nine species of fir and at least four species of adelgids that attack fir.

There are about 10 species of hemlock in the world; two are native to western North America and two are native to eastern North America. The other species of hemlock are distributed in Asia. The genus is not present in Europe. The only species of adelgid known to attack hemlock, *A. tsugae*, is native to Asia but is now found wherever hemlock occurs.

Hemlock and fir in eastern North America may occur in homogeneous patches that foster the survival of wind-dispersed adelgids. Hemlocks in Asia are restricted to narrow bioclimatic zones on steep slopes in rugged mountainous terrain and grow scattered in stands where other species dominate. This is in marked contrast to *T. canadensis*, which does not have exacting soil requirements and can be the dominant species in stands so dense that an understory is not able to develop (Godman and Lancaster 1990). Fir trees in Europe also are located on steep slopes. It has been suggested that the wind patterns and the discontinuity of the fir stands in this terrain are less favorable for the survival of wind-dispersed *A. piceae* than are conditions in the vast forests of balsam fir in the relatively flat areas of eastern Canada and Maine (Wellington 1976).

Harmless at home

The following three examples illustrate how adelgids are harmless to the hosts on which they have co-evolved, but when introduced to a new host can severely damage or even kill it.

Adelges piceae

Adelges piceae is an example of an adelgid changing its feeding behavior on a new host and harming it. In Europe, it causes little harm to *Abies alba*. The trunks and larger branches of trees older than 30 years are preferred and can be completely covered with the white bodies of the adelgid in outbreaks. After its introduction to North America near the turn of the century *A. piceae* spread rapidly through most areas where fir grows on the continent. It feeds on most of the species of fir in North America, but is especially injurious to the eastern species. It feeds on stems and at the base of buds of *A. balsamea* and *A. fraseri* causing extensive swelling of the shoots near the buds (gout disease) and the formation of compression wood (rotholz), which causes transpiration stress that can result in tree death (Hain 1988).

Adelges nordmannianae

Adelges nordmannianae (Eckstein) is an example of an adelgid causing severe harm when its feeding is on a different part of the new host than that of an endemic adelgid. This adelgid is thought to be endemic to the region of the Caucasus Mountains (Turkey, Georgia, Kazhakstan). There it feeds on small branches, twigs, and needles of *Abies nordmannianae* and other firs restricted to the region. It seldom causes harm to these trees. The adelgid has been introduced to other parts of Europe where *A. alba* occurs. The typical form of this adelgid infests

branches, twigs, and needles of young *A. alba* which causes deformities and tree death. Another form that behaves like *A. piceae* infests the trunks of mature *A. alba* and causes little harm (Eichhorn 1968).

Adelges tsugae

Adelges tsugae is extremely damaging to some new species and harmless to others, but appears to have the same feeding behavior on all species. It is innocuous in its endemic area, Asia. It also causes little harm to the two species of hemlock in western North America, but causes severe damage to the two species endemic to eastern North America. Phylogenetic relationships within *Tsuga* do not seem to relate to the vulnerability of species to *A. tsugae*. A recent DNA analysis of *Tsuga* shows two sister lineages, one for the western hemlocks, *T. mertensiana* and *heterophylla*, and another for the other species (B. LePage, Univ. Pennsylvania, pers. comm.). The preferred feeding site on all hemlock species seems to be the current year's growth with older tissue fed on to a lesser extent.

Natural enemies

Adelges piceae

Because of the economic importance of *A. piceae*, its natural enemy complex in Europe has been studied extensively. A major effort was made by Canada from 1934 to 1969 to establish biological control by importing natural enemies from Europe. Details of this work can be found in Clark et al. (1971) and Schooley et al. (1984). Most of the species imported to Canada were subsequently released in the United States (Clausen 1978). More than 30 species of predators were imported, and eight of these were recovered a year or more after release. The following six species were the focus of this work: *Leucopis* nr. *obscura* Hal. (Diptera: Chamaemyiidae), *Cremifania nigrocellulata* Czerny (Diptera: Chamaemyiidae), *Aphidoletes thompsoni*, Möhn (Diptera: Cecidomyiidae), *Laricobius erichsonii* Rosenhauer (Coleoptera: Derodontidae), *Aphidecta oblitterata* (L.) (Coleoptera: Coccinellidae), and *Scymnus* (Pullus) *impexus* (Mulsant) (Coleoptera: Coccinellidae) Montgomery and Lyon (1996) give a brief analysis of the biology and factors that may influence the success of these species as biological control.

Twenty-one species of predators were released in stands of Fraser fir in North Carolina. The climate and feeding habits of *A. picea* in the Southern Appalachians likely would be more favorable for the predators than eastern Canada and Maine. Unfortunately, 15 of the species came from Pakistan and India, which have a very different climate from that of the release site. None of the predators from Asia were recovered the next year following release (Amman and Spears 1971). The above listed six species of predators from Europe also were released, and three of these (*A. thompsoni*, *A. oblitterata*, and *L. erichsonii*) were recovered the following year and thought to be established (Amman and Spears 1964). I am not aware of any subsequent reports of these predators in the Southern Appalachians.

Several reasons have been offered for the lack of success of biological control of *A. piceae* in North America. First, the predators that attack *A. piceae* in Europe are a complex of species that would be difficult to establish. Second, the phenology of the predators in the complex is sequential and well synchronized with the host (Eichhorn 1968), and this synchronization may be disrupted in a different climate. Third, the predators attacking dense stem populations in central Europe seem to be inversely density dependent (Eichhorn 1968) and are more effective in finding and regulating small, dispersed populations. An example is *Scymnus* (Pullus) *impexus*, which is very effective at reducing spot populations but has little effect on outbreaks in Europe.

At the end of the program to obtain biological controls for *A. piceae* in North America, Eichhorn (1969) explored the Caucasus Mountains in Turkey, where the endemic adelgids feed mainly on the twigs, rather than the stems of fir as in western Europe. Predators typical of stem infestations such as *Laricobius* sp. and *Cremifavia* sp. were absent. The most important predators were Diptera and Coccinellidae. Early in the season on 40 current year branches, the adelgid population consisted of 585 adults and 24,100 eggs. Also present were 69 eggs and larvae of an unidentified *Leucopis* sp. and 10 syrphid larvae. In three weeks, 93% of the adults had been destroyed and <4000 eggs were left. At this time the larvae of *Leucopis* sp. had pupated, but larvae of the lady beetle *Aphidecta oblitterata* were observed feeding on the remaining adelgid adults and eggs. Eichhorn felt that the *Leucopis* sp. should be introduced to North America because it would complement the action of other species previously introduced.

Adelges tsugae

Until recently, nothing was known about the natural enemies of *A. tsugae* in Asia. Based on field investigations in 1992 in Japan, McClure (1995a) reported the adelgid was kept at low levels by a complex of five natural enemies: a lacewing (vr. *Mallada prasina* [Burm.]), a cecidomyiid midge fly (*Lestodiplosis* sp.), an unidentified syrphid fly, a lady beetle (*Pseudoscymnus tsugae* Sasaju & McClure), and an oribatid mite (*Diapterobates humeralis* Hermann). The mite did not actually feed on the adelgid, but consumed the woolly wax that covers the ovisacs. This dislodged the eggs, which fell to the forest floor, where they desiccated or were attacked by ground biota (McClure 1995b). This mite is widely distributed in the Northern Hemisphere and is reported to feed mainly on hyphae and spores of higher fungi (Behan and Hill 1978). The mite was imported and released in Connecticut and was reported to have overwintered and spread in a hemlock forest (McClure 1995a). The status of this mite is unclear. McClure's focus has shifted to the lady beetle, *P. tsugae*. It feeds on all stages of the adelgid, and several generations per year can be reared in the laboratory. (Cheah and McClure 1996).

In 1995, with Chinese cooperators, I began explorations for natural enemies of *A. tsugae* in the People's Republic of China. The adelgid and

a complex of its natural enemies were found everywhere at elevations of 2,400 to 2,900 meters in western Sichuan and northwestern Yunnan where *Tsuga dumosa* and *T. forestii* grow. Predators in the families Coccinellidae, Cecidomyiidae, Syrphidae, Chrysopidae, Chamaemyiidae, Anthrocoridae, and Inocellidae were found (Wang et al., in press). Efforts focused on the extraordinary diversity of lady beetles present in the forests with hemlock. More than 50 species of lady beetles have been collected from adelgid-infested hemlock trees in China, 21 of which are new to science (Yu et al. 1998). Nine of these beetles are recognized as predators of *A. tsugae*.

Two of the newly discovered species in China, *Scymnus sinuanodulus* Yu and Yao (see Figure 1), and *S. camptodromus* Yu and Liu, have been imported to the United States. Host range evaluations done in the field in China and in the USDA Forest Service's Quarantine Laboratory indicate that *S. sinuanodulus* prefers adelgids, but will feed on small, immobile aphids if starved (Montgomery et al. 1998). This lady beetle seems a good, safe candidate for biocontrol of *A. tsugae*; it should be most effective at preventing small, spotty infestations from developing to large harmful populations.



Figure 1. *Scymnus sinuanodulus*, Yunnan, China. Photo by M.E. Montgomery, USDA Forest Service, Hamden, CT.

Several incumbent predators have been collected from *A. tsugae* in Connecticut (Montgomery and Lyon 1996). The most abundant predators were *Scymnus suturalis* Thunberg and the derodontid beetle *Laricobius rubidus* LeConte. The former species is native to Europe and apparently was both accidentally and deliberately introduced. It is frequently recovered from *Pinus sylvestris* (Scotch pine) infested with *Pineus* sp. in Europe and the United States. *L. rubidus* is commonly found on white pine infested with *P. strobi*. Both species are present on hemlock in the spring and fall but do not have a substantial impact. Brown lacewing, midge, and syrphid larvae are found in low numbers. Several other coccinellids are present, but these may be feeding on scale insects. I am finding the exotic lady beetle, *Harmonia axyridis* Pallas, at increasing levels on hemlock, but it feeds little on the adelgid (Montgomery et al. 1998).

Pineus strobi

The pine bark adelgid is a common native species in eastern North America that has spread to other parts of the world. The only other native adelgid species in eastern North America, *Pineus pinifoliae* and *P. floccus*, have not been well studied. The most common predators of *P. strobi* are *L. rubidus* and the chamaemyiid fly, *Leucopus pinicola* Mall. (Clark and Brown 1957). Other predators include the syrphid fly, *Syrphus torvus* O.S., several midges, and the true bug, *Tetraneura americana* Pars. (Raske and Hodson 1964). Another native predator of *P. strobi*, *Leucopina americana*, may have been affected by the introduction

of predators to control *A. piceae*. It established on *A. piceae* but did not become numerous following its introduction. Since the introduction of a related species, *Leucopis obscura* Haliday, to control *A. piceae*, *L. americana* has been found less frequently (Brown and Clark 1957).

Several native predators have been reported to attack *A. piceae* in Canada (Brown and Clark 1956), in the northeastern United States (Mitchell 1962), and in the Southern Appalachians (Amman 1970). These are surprisingly long lists, totaling more than 30 species in 10 families and 8 orders, and include mites and even slugs. Many of the species on the list appear to be generalists. Mites on Fraser fir in the Southern Appalachians were the predominant predator of *A. piceae*, and one species showed a positive numerical response; however, the impact of all predator species in total was negligible (Amman 1970).

Summary

The evolutionary isolation of fir and hemlock in eastern North America from adelgids has resulted in their high vulnerability to these insects. I use the term *vulnerability* because adelgids that have co-evolved with their hosts can reach high populations on the host and not harm it. The proper term for these hosts is *tolerant*, which means that the host suffers little damage, rather than *resistant*, which implies that the host is unsuitable for feeding or development of a potential parasite.

Adelgids, when at home in their endemic habitat, are associated with a complex of predators. Adelgids have no known parasites, which generally have faster numerical responses than predators. Populations of *A. piceae* in central Europe often outbreak, and the natural regulation seems to be deficient in fast, density-dependent numerical response. Predators such as *Leucopia* sp., with faster numerical response, have been found in the Caucasus Mountains of Turkey.

Unlike *A. piceae* on silver fir in Europe, high populations of *A. tsugae* are rare on hemlock in Asia. Detailed studies have not been done on the regulatory impact of *A. tsugae* predators in Asia, but I feel that Diptera are the principal, fast-acting agents, and lady beetles are the primary agents that maintain populations at low levels.

Recommendations for control

Control of *A. piceae* on Fraser fir probably can be achieved best by developing tolerance. Fraser fir exists in six discontinuous areas that are genetically distinct (Hain 1988). Mortality has been less in the more northern areas but this may be due to site factors. Tolerance tests to *A. piceae* could easily be done on provenances in a nursery. Hain et al. (1991) provides a review of the work he and others have done on the physical and biochemical mechanisms of tolerance in fir.

The possibility of promoting tolerance in Fraser fir is appealing, since it involves transplanting or selecting for endemic genotypes rather than creating tolerant hybrids through crosses with an exotic species. While additional attempts to achieve classical biological control of *A. piceae* on Fraser fir are of a lesser priority, further survey of the incumbent natural enemies attacking *A. piceae* on Fraser fir should be done. Mites have been overlooked as adelgid predators, and their impact should be considered in surveys of the natural enemies of other adelgids as well.

Control of *A. tsugae* on eastern and Carolina hemlock will most likely be achieved through a combination of increased host resistance and biological control. Although the other species of hemlock seem to have more resistance than the eastern hemlocks, it would take many years to create a resistant genotype through a series of hybridization and backcrosses. A major hindrance may be that the other species of hemlock have more exacting soil and climate requirements than *T. canadensis*; hence, developing a genotype that is both resistant and adaptable to a range of sites may be difficult.

Efforts to establish biological control of *A. tsugae* are under way. Small lady beetles in the subfamily Scymniinae are promising. It is unlikely that these will compete or impact native predators of adelgid, since the niche occupied by members of this subfamily seems vacant in eastern North America. One problem is that Scymniinae tend to develop local populations of distinct species; hence they may not adapt well to new environments. The coccinellids are only part of the regulation of *A. tsugae* in Asia. Increased efforts need to be made to identify the Diptera associated with the occasional dense populations found at branch tips in China. The success of the program would be improved by long-term studies of the dynamics of *A. tsugae* and its predators was not done prior to the release of natural enemies in North America. A survey of native natural enemies should be done in the Southern Appalachians prior to the release of exotic predators. Except for the coccinellids, for which there are taxonomic specialists in Asia, a major impediment is the availability of specialists to identify adelgid natural enemies.

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List of Acronyms

ARS - Agricultural Research Service (USDA)

BRD - Biological Resource Division (USGS)

DOI - U.S. Department of the Interior

IUFRO - International Union of Forestry Research Organizations

NBCI - Natural Biological Control Institute (USDA)

NRPP - Natural Resource Protection Program

SAFL - Southern Appalachian Field Laboratory

SAMAB - Southern Appalachian Man and Biosphere Program

USDA - U.S. Department of Agriculture

USGS - U.S. Geological Survey

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